Genetic evaluation of Angus cattle for carcass marbling using ultrasound and genomic indicators[1]

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ABSTRACT: The objectives were to estimate genetic parameters needed to elucidate the relationships of a molecular breeding value (MBV) for marbling, intramuscular fat (IMF) of yearling bulls measured with ultrasound, and marbling score (MRB) of slaughtered steers, and to assess the utility of MBV and IMF in predicting the breeding value for MRB. Records for MRB (n = 38,296) and IMF (n = 6,594) were from the American Angus Association database used for national cattle evaluation. A total of 1,006 records of MBV were used in this study. (Co)variance components were estimated with ASREML, fitting an animal model with fixed contemporary groups for MRB and IMF similar to those used in the Angus national genetic evaluation. The overall mean was the only fixed effect included in the model for MBV. Heritability estimates for carcass measures were 0.48 ± 0.03, 0.31 ± 0.03, and 0.98 ± 0.05 for MRB, IMF, and MBV, respectively. Genetic correlations of IMF and MBV with MRB were 0.56 ± 0.09 and 0.38 ± 0.10, respectively. The genetic correlation between IMF and MBV was 0.80 ± 0.22. These results indicate the MBV evaluated may yield a greater genetic advance of approximately 20% when used as an indicator trait for genetic prediction of MRB compared with IMF. However, neither of these indicators alone provides sufficient information to produce highly accurate prediction of breeding value for the economically relevant trait MRB. Given that the goal is a highly accurate prediction of true breeding value for MRB, results of this work point to the need to 1) continue progeny testing, and 2) continue increasing the genetic correlation between the MBV and MRB.

Key words: beef cattle, genetic parameter, marbling, molecular breeding value, ultrasound

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INTRODUCTION

Price discrimination based on quality grade provides an economic incentive for selection of breeding stock based on carcass merit. Since 1974, the American Angus Association (**AAA**) has collected data for genetic evaluation of carcass traits (Wilson et al., 1993). Since 1997, this genetic evaluation has been augmented with intramuscular fat (**IMF**) measured on yearling bulls and heifers by using ultrasound. Recently, these data have been analyzed jointly in a system of national cattle evaluation (**NCE**) for the economically relevant trait marbling (**MRB**; MacNeil and Northcutt, 2008). Commercial firms genotype animals for breeders and also may provide estimates of molecular breeding value (**MBV**) based on multiple genetic markers. To date, use of genetic markers and MBV has been in tandem with results of the NCE. This approach is not optimal, and if both phenotypic and molecular data are available, their joint consideration is the most powerful selection strategy (Dekkers and Hospital, 2002; Spangler et al., 2007). Thallman (2004) put forth a vision that incorporated molecular data in the NCE to produce a more accurate evaluation of genetic merit than is currently produced based on phenotypic data alone. Our objectives were to estimate the genetic parameters needed to elucidate the relationships of one such MBV with IMF and MRB, and to assess the utility of these indicators in predicting the true breeding value for MRB.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were extracted from existing AAA databases.

Carcass data were either from an AAA-sponsored sire evaluation program or submitted directly by mem-

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bers who had obtained the data by using a variety of commercial and private services. Dams were predominantly commercial Angus-type cattle. However, unique identification of dams was not required; thus, dams were considered unknown. The AAA defines carcass contemporary group as the concatenation of herd code, slaughter date, breeder group code, and sex. Marbling score (5 = Small^0, 6 = Modest^0, 7 = Moderate^0, and so on; Beef Improvement Federation, 2002) was adjusted to 480 d of age at slaughter. A total of 59,124 records were available, and 38,296 remained after editing to remove 1) all heifers and bulls, 2) contemporary groups of fewer than 30 animals, 3) sire groups of fewer than 7 animals, and 4) observations more than 4 SD from their respective contemporary group mean. Thus, the 38,296 MRB records used herein were from steer calves by 1,470 Angus sires, and there were 748 contemporary groups.

The MBV examined herein were developed by Igenity (Igenity is a registered trademark of Merial Limited, Duluth, GA, in the United States and elsewhere) specifically for Angus cattle. Physiological and positional candidate genes and QTL for MRB from numerous previous studies were used to direct a search for the SNP subsequently used herein. Candidate genes included diacylglycerol *O*-acyltransferase (Grisart et al., 2001; Thaller et al., 2003), leptin (Buchanan et al., 2002; Kononoff et al., 2005; Chung et al., 2008), mitochondrial transcription factor A (Jiang et al., 2005), stearoyl-CoA desaturase (Jiang et al., 2008a), and urotensin 2 and its receptor (Jiang et al., 2008b). Additional loci of interest were identified from studies identifying QTL (e.g., MacNeil and Grosz, 2002; Casas et al., 2003; Alexander et al., 2007). Additional SNP were also identified in house by Merial Ltd. In all, genotypes from 444 Angus sires, for a total of 114 SNP, were evaluated for their univariate associations with the EPD for MRB published by AAA in 2008. The effect of each marker was estimated as a regression on the number of copies of one of the alleles of the marker. For simplicity, the number of copies of the first allele was assigned (based on alphabetic order) 2, 1, or 0 such that genotypes CC, CT, and TT from a C/T mutation were coded as 2, 1, and 0, respectively. Similarly, genotypes AA, AG, and GG from an A/G mutation were coded as 2, 1, and 0, respectively.

After the single-marker analysis, each SNP that gave an indication of being at least tentatively associated with the trait ($P < 0.10$) was evaluated further to determine its contribution to the overall prediction of EPD for MRB. All the chosen SNP were evaluated in pairs for potential linkage disequilibrium (**LD**). High LD ($r^2 > 0.80$) between 2 SNP implies that both are potentially marking the same QTL. To avoid redundancy, only 1 of the pair was chosen as a tag SNP to capture the effect of the QTL in question (Carlson et al., 2004). The final model for computing MBV was set up as a 40-marker compound covariate prediction equation (Tukey, 1993), with covariates made up of the 2, 1, and 0 codes for the genotypes of each marker and the weights constituting the corresponding allele substitution effect estimated from each marker. Animals whose MBV data were used in this study were not used in the marker panel development process. Records of MBV from 1,006 animals were used in this study.

Ultrasound images were collected by certified field technicians. Results from ultrasonic scanning of yearling Angus bulls were interpreted through centralized processing laboratories and reported to AAA for use in genetic evaluation of IMF. Records were adjusted by AAA to 365 d of age. For IMF, the AAA defines contemporary group as the concatenation of breeder herd code, weaning herd code, image processing date, calf type (embryo or natural), scanning date, technician, breeder group code, test type, sex, and diet. The IMF data set was limited to those bulls having an MBV and their contemporaries. Thus, 6,594 IMF records from calves by 669 sires were used herein, and there were 250 contemporary groups.

The 4-generation pedigree for all animals having a record of MRB, IMF, or MBV was extracted from the herdbook of the AAA. A total of 195 sires had progeny with records of both MRB and IMF. A total of 127 sires with MBV had progeny with records of MRB. Finally, 717 animals had both IMF and MBV in the data.

The linear model used to estimate genetic variances and covariances can be described as

$$\begin{bmatrix}\mathbf{Y}_1\\ \mathbf{Y}_2\\ \mathbf{Y}_3\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1\boldsymbol{\beta}_1\\ \mathbf{X}_2\boldsymbol{\beta}_2\\ \mathbf{X}_3\boldsymbol{\beta}_3\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_1\mathbf{u}_1\\ \mathbf{Z}_2\mathbf{u}_2\\ \mathbf{Z}_3\mathbf{u}_3\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\\ \mathbf{e}_3\end{bmatrix},$$

where the $\mathbf{Y}_i$ are vectors of MRB, IMF, and MBV, respectively; and $\mathbf{X}_i$ and $\mathbf{Z}_i$ are design matrices relating the data to their respective fixed contemporary group effects ($\boldsymbol{\beta}_i$), random animal effects ($\mathbf{u}_i$), and random residual effects ($\mathbf{e}_i$). Note that the only contemporary group for MBV corresponded to the overall mean. The random animal effects were assumed to have null means and variances:

$$\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\\ \mathbf{u}_3\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma^2_{u_1} & \mathbf{A}\sigma_{u_1u_2} & \mathbf{A}\sigma_{u_1u_3}\\ \mathbf{A}\sigma_{u_2u_1} & \mathbf{A}\sigma^2_{u_2} & \mathbf{A}\sigma_{u_2u_3}\\ \mathbf{A}\sigma_{u_3u_1} & \mathbf{A}\sigma_{u_3u_2} & \mathbf{A}\sigma^2_{u_3}\end{bmatrix},$$

where **A** represents the numerator relationship matrix. The random residual effects were assumed to have variances

$$\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\\ \mathbf{e}_3\end{bmatrix} = \begin{bmatrix}\mathbf{I}\sigma^2_{e_1} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}\sigma^2_{e_2} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma^2_{e_3}\end{bmatrix},$$

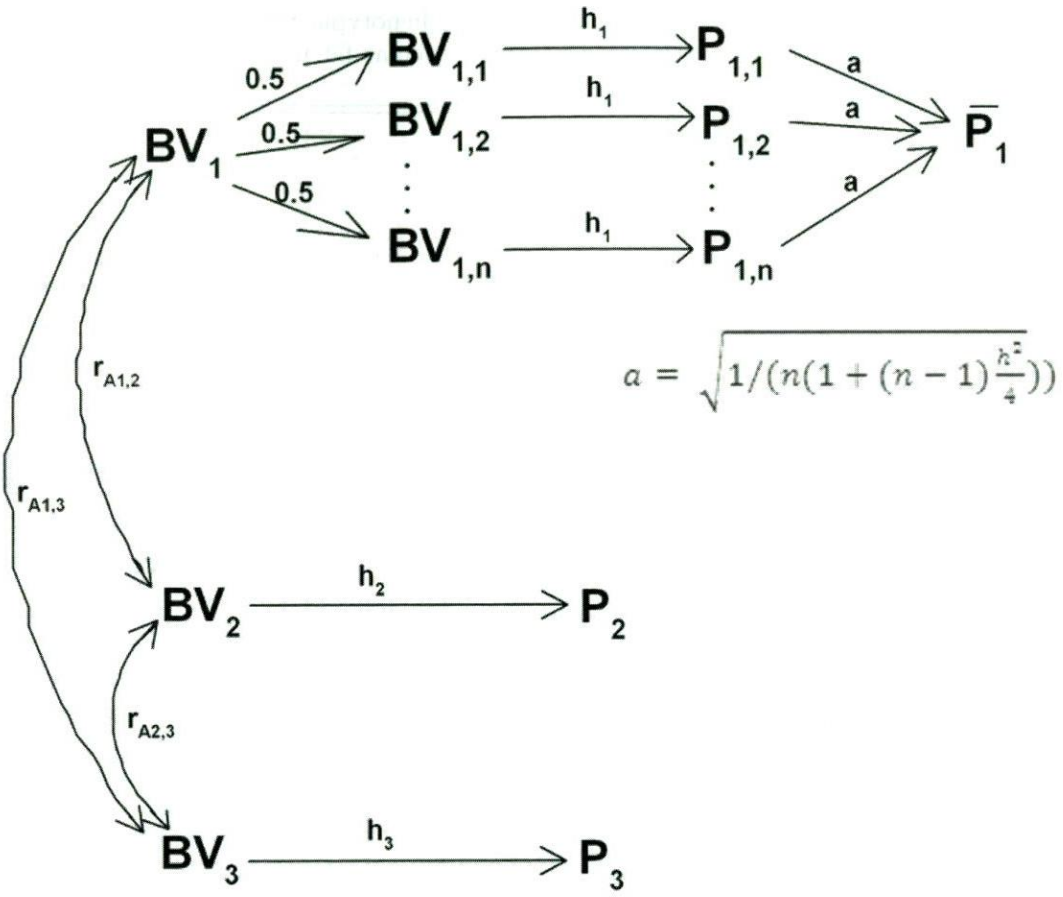

Figure 1. Path diagram illustrating genetic relationships among the economically relevant trait carcass marbling of steer progeny (subscript 1), intramuscular fat of yearling bulls measured with ultrasound (subscript 2), and molecular breeding value of bulls (subscript 3). h_i = square root of heritability for trait i; $r_{Ai,j}$ = genetic correlation of traits i and j; BV_i = true breeding value of an individual for trait i; $BV_{1,i}$ = breeding value for carcass marbling of the ith progeny; $P_{1,i}$ = carcass marbling phenotype of the ith progeny, with average $\bar{P}_1$; n = number of progeny; P_2 and P_3 = phenotypes for intramuscular fat of yearling bulls measured with ultrasound and the molecular breeding value, respectively.

where **I** represents an identity matrix appropriate to the number of observations for the traits being analyzed. Estimates of the variance and covariance components and associated estimates of heritability and their SE were obtained using ASREML version 2.0 (Gilmour et al., 2006). The genetic model assumed to represent the relationships among MRB, IMF, and MBV is presented as a path diagram in Figure 1. Trade-offs among the different sources of information used to predict the breeding value for the economically relevant trait MRB were assessed using standard formulas for accuracy (e.g., Van Vleck, 1993) and parameter estimates obtained as described above, and assuming a constant selection intensity.

Subsequent to estimating the variance components, a set of 4 BLUP analyses were conducted to predict EPD for MRB. All these analyses used the same pedigree as described above. The first analysis was a single-trait analysis of MRB. The second and third analyses were bivariate analyses of MRB with IMF and MRB with MBV. Finally, a trivariate analysis of MRB, IMF, and MBV was conducted. In each of these analyses, accuracy of the EPD for MRB was calculated following Beef Improvement Federation (2002) guidelines. These analyses were used to summarize the improvement in accuracy resulting from additional information arising from ultrasonic scanning and MBV.

RESULTS AND DISCUSSION

Summary statistics describing the data sets are presented in Table 1. Median birth year of the steers from which carcass data were obtained was 1997, with 90% of the data coming from steers born between 1991 and 2003. These steers were the progeny of 1,275 sires. Median birth year of the bulls from which data were collected using ultrasound was 2001 and 90% of these data came from calves born between 1998 and 2005. The EPD for MRB of animals used to develop the MBV averaged 0.23, with SD of 0.25, and had accuracies ranging from 0.15 to 0.93; average accuracy was 0.41. Because the MBV was developed using relatively low-accuracy marbling EPD, the contributing SNP should be periodically reevaluated as new data become available.

The average relationship among animals used to develop the MBV was 6.84%, with 5th and 95th percentile values of 1.10 and 17.26%, respectively. The aver-

Table 1. Numbers of observations, means, and phenotypic SD for the economically relevant trait marbling and the indicators intramuscular fat percentage and molecular breeding value

Trait	N	Mean	SD
Carcass marbling score[1]	38,273	6.05	0.89
Ultrasound intramuscular fat content, %	6,594	3.91	0.73
Molecular breeding value	1,006	1.13	0.08

[1]5 = Small^0, 6 = Modest^0, 7 = Moderate^0, and so forth (Beef Improvement Federation, 2002).

age relationship between animals used to develop the MBV and those animals used for variance component estimation was 6.19%, with 5th and 95th percentile values of 1.52 and 14.4%, respectively. Eighty-five of the animals used for variance component estimation were among the 240 Angus bulls having 100 or more progeny recorded in 2008. These results may be interpreted to suggest some general applicability of the MBV for predicting MRB across a broad range of Angus cattle.

Shown in Table 2 are estimates of genetic (co)variances and parameters derived from them for MRB, IMF, and MBV for marbling. The estimates for MRB and IMF are consistent with those calculated from a larger sample from the same database and reported previously by MacNeil and Northcutt (2008). The present estimate of heritability for MRB is consistent with the 0.46 average from 17 studies reviewed by Bertrand et al. (2001), whereas presently estimated heritability for percentage of IMF measured using ultrasound was less than the corresponding average of 0.41 reported by Bertrand et al. (2001). The extraordinarily large heritability estimate for MBV reflects its being formulated from only additive genetic effects of the SNP. As would be expected from the positive genetic trend for marbling in Angus cattle (MacNeil and Northcutt, 2008) and the positive genetic correlation between MRB and MBV reported here, the MBV also increases with birth year.

The presently estimated genetic correlation between MRB and IMF (0.56) approached the range (0.59 to 0.80) reported by others (Devitt and Wilton, 2001; Crews et al., 2003; Meyer, 2007), the 0.90 estimate of Kemp et al. (2002) notwithstanding. All evidence suggests that IMF is a useful predictor of MRB. Using the rule of thumb proposed by Robertson (1959) that estimated genetic correlations $\geq$0.8 indicate alternative measures of the same trait may indicate redundancy of IMF and MBV. However, this conclusion should be tempered by the sizeable SE of the estimate. The genetic correlation of MBV with MRB was somewhat less than that between IMF and MRB. The Beef CRC (2009) also found positive correlations of various degrees (0.02 to 0.19) between a Pfizer Animal Genetics molecular value prediction and the Australian carcass MRB in 4 different types of breed groups. Based on the present analyses, evaluation of predicted correlated responses to selection suggests that use of the MBV would result in a 20% greater predicted response in carcass MRB than use of IMF in mass selection. This seeming contradiction between the magnitudes of the genetic correlations and the utility in selection for MRB can be explained by the much greater estimated heritability of MBV than IMF. However, in predicting breeding values, records of MBV from relatives do not increase accuracy, whereas IMF records from relatives improve the accuracy of prediction (Beef CRC, 2009). Thus, the calculated 20% advantage from using MBV would shrink dramatically if there were, for example, IMF records from 10 paternal half sibs.

It should be recognized from Figure 1 that in the present study, neither IMF nor MBV is expected to provide as much information about the breeding value of an animal for MRB as 2 progeny in a well-designed progeny test. However, progeny testing prolongs the generation interval and increases the cost of evaluating candidates for selection. Following Garrick (2007) in

Table 2. Estimates of additive genetic variance and heritability ($h^2 \pm$ SE) for the economically relevant trait marbling score and the indicators intramuscular fat percentage and molecular breeding value (on the diagonal), genetic covariances among traits (above diagonal), and genetic correlations ($r_g \pm$ SE) derived from them (below diagonal)

Trait	Marbling score	Intramuscular fat percentage	Molecular breeding value
Marbling score	0.3812 0.48 ± 0.03	0.1404	0.0179
Intramuscular fat percentage	0.56 ± 0.09	0.1663 0.31 ± 0.03	0.0253
Molecular breeding value	0.38 ± 0.10	0.80 ± 0.22	0.0060 0.98 ± 0.05

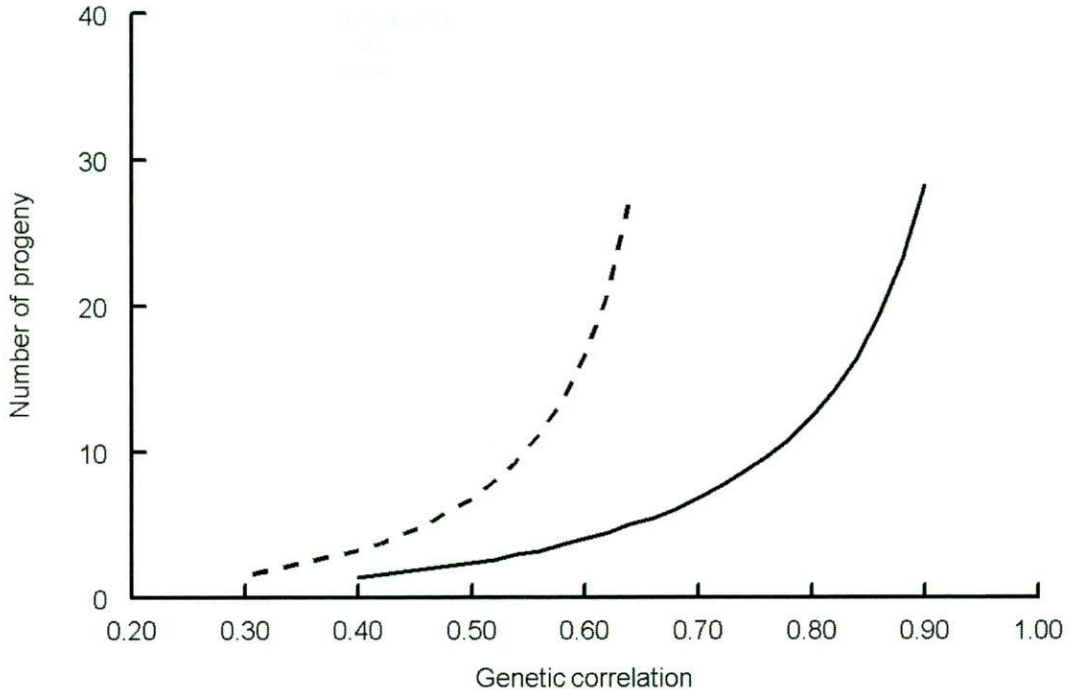

Figure 2. Trade-off between genetic correlation of molecular breeding value with marbling and number of progeny with phenotypes evaluated. The solid line represents equal genetic gain per generation and the dashed line represents equal genetic gain per year.

holding selection intensity constant but reducing the generation interval for sires from 5.5 yr with progeny testing to 2.5 yr with MBV or ultrasonic scanning of yearling bull candidates for selection, the indirect measures produce rates of expected annual genetic progress equivalent to a progeny test with approximately 4 or 5 offspring, respectively. This analysis can be extended to more generally address the trade-off between the magnitude of the genetic correlation and the number of tested progeny (Figure 2). This analysis may be interpreted to suggest that as the genetic correlation between MBV and MRB approaches 0.6, there may be a disincentive to continue collecting phenotypic data. However, continued collection of phenotypic data is needed to update the EPD and MBV for changes in allele frequency resulting from selection.

For progeny-tested sires, for which accuracy of their EPD for MRB averaged 0.47, including either IMF or MBV in the prediction of EPD for MRB resulted in essentially no further increase in accuracy. For those animals that were not progeny-tested sires and that had only an IMF record themselves (n = 5,869), accuracy of the EPD for MRB increased from 0.11 to 0.15 with the inclusion of IMF records in the analysis. Accuracy of the MRB EPD for animals that were not progeny-tested sires and that had only an MBV record themselves (n = 276) increased from 0.12 to 0.18 when the MBV records were included in the analysis as an indicator trait. Finally, for those animals that were not progeny-tested sires but that had records of both IMF and MBV (n = 710), accuracy of the MRB EPD increased from 0.07 to 0.12 and 0.13, respectively, when either indicator trait was included in the analysis. Finally, for this latter set of animals, when both IMF and MRB were included as indicator traits, accuracy of the MRB EPD was further increased to 0.15.

Use of ultrasound on candidates for selection at approximately 1 yr of age can increase the accuracy of genetic evaluation of yearling bulls for MRB and a shortened generation interval relative to progeny testing. So too, use of an efficacious MBV offers additional potential to reduce the cost of testing by providing increased accuracy of genetic evaluation for MRB either shortly after conception (by using DNA from embryos) or at birth. This reduction in cost arises from the opportunity to implement sequential culling more effectively. Compared with ultrasonic scanning, use of MBV does not affect the generation interval because, with either technology, the generation interval is constrained by growth and sexual maturation of potential candidates for selection.

Given that the goal is a very accurate prediction of true breeding value for MRB, results of this work point to the need to 1) use progeny testing, and 2) increase the genetic correlation between the MBV and MRB. However, results from dairy cattle, based on substantially greater genetic correlations than those found here, suggest that breeding values derived solely from genomic information may supplant the use of progeny testing entirely (Hayes et al., 2009). The genetic correlation between MBV and an economically relevant trait may be increased by increasing the LD between markers and QTL or, in the extreme, by identifying the causative mutations at QTL, increasing the number of animals with phenotypes and genotypes used to derive MBV, sampling the intended target population more

accurately, and increasing the accuracy of predictions of true breeding value used to derive the MBV.

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